



Variability in trunk segmentation in the centipede order Scolopendromorpha: a remarkable new species of *Scolopendropsis* Brandt (Chilopoda: Scolopendridae) from Brazil

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Abstract

Of the two centipede orders that complete segmentation during embryogenesis, most species belonging to Geophilomorpha have an intraspecifically variable number of trunk segments, whereas those of the Scolopendromorpha have been assumed to have a fixed segment number, with minor variation (21 or 23 segments) across the group as a whole. Trunk segment numbers are used as a taxonomic character as high as the familial or subordinal level in Scolopendromorpha. The first known instance of variability in trunk segment numbers within a scolopendromorph species has recently been proposed for the Brazilian *Scolopendropsis bahiensis* (Brandt, 1841), which has either 21 or 23 segments in different parts of its geographic range. Here we document a closely related scolopendrid from Tocantins State, central Brazil, *Scolopendropsis duplicata* n. sp., which differs from *S. bahiensis* in having either 39 or 43 segments. This unique segment count is incorporated into a revised diagnosis of the order Scolopendromorpha. The deeply nested position of *Scolopendropsis* within the Scolopendridae implies that the geophilomorph-like trunk segment number in *S. duplicata* is convergent with similar segmentation in Geophilomorpha.

Key words: Chilopoda, trunk segmentation, Scolopendrinae, taxonomy, Tocantins

Introduction

Centipedes of the order Scolopendromorpha exhibit minor interspecific variability in segment numbers, until now all known species having either 21 or 23 leg-bearing trunk segments. The two alternative states have been regarded as phylogenetically conservative and are given considerable taxonomic weight in current classificatory schemes, i.e., in part used to divide the Scolopendromorpha into families (Shelley 2002) or even a basal split in the order between 21- and 23-segmented groups (Schileyko 1992).

Fundamental to the taxonomic importance assigned to 21- versus 23-segmented conditions in different scolopendromorph lineages is the observation that trunk segment numbers are invariant within species. The factual basis for this observation has recently been challenged for the first time. The first claim of a variable number of segments within a scolopendromorph species was made by Schileyko (2006) in the case of a scolopendrid from Brazil, *Scolopendropsis bahiensis* (Brandt, 1841). The type material of this species has 23 leg-bearing trunk segments, but following its recent taxonomic revision, *S. bahiensis* has been shown to have 21 segments throughout most of its geographic range, which includes southeastern, northeastern and central Brazil, in the cerrado and caatinga biomes, as well as the Atlantic forest. The 21-segmented populations had for-

merly been identified as a different species and, indeed, as a member of a different genus, *Rhoda calcarata* (Pocock, 1891), but were shown to be identical to the type material of *Scolopendropsis bahiensis* in all respects except for the two additional trunk segments (Schileyko 2006). *Scolopendropsis* Brandt, 1841, provides unequivocal evidence that trunk segmentation is variable within a restricted clade of Neotropical Scolopendridae, and is reasonably regarded as variable within a single species.

Elsewhere in the Chilopoda, intraspecific variability in trunk segment numbers is confined to Geophilomorpha, the sister group of Scolopendromorpha (Edgecombe 2007 and references therein) in a clade united by epimorphic development, i.e., hatching from the egg with the complete adult complement of body segments. Indeed, with a few exceptions among the most segment-rich species of the genus *Mecistocephalus* Newport, 1843 (Bonato *et al.* 2001, Uliana *et al.* 2007), variable segment counts are confined to one of the two basally diverging lineages within the Geophilomorpha, the Adesmata. The other chilopod orders, Scutigermorpha, Lithobiomorpha, and Craterostigmomorpha, all have a fixed number of 15 trunk segments, the primitive number for Chilopoda as a whole (Minelli *et al.* 2000).

Our understanding of centipede body plans has assumed that 23 segments is the maximum in non-geophilomorphs and counts of 27 or more evolved only once, in the stem-species of Geophilomorpha. Herein we report a new species from Brazil that demonstrates a convergent evolution of a multisegmented trunk within the Scolopendromorpha, and forces a revised ordinal diagnosis to include species with as many as 39 or 43 segments.

Systematic position of *Scolopendropsis duplicata* n. sp.

Scolopendropsis duplicata n. sp., described below, is a scolopendrid with either 39 (Fig. 1) or 43 pairs of trunk legs. Its geophilomorph-like trunk segmentation can be viewed as either, 1) homologous between Scolopendromorpha and Geophilomorpha, in which case *S. duplicata* is necessarily ascribed a pivotal, basal position in scolopendromorph phylogeny, or 2) convergent between Scolopendromorpha and Geophilomorpha. We argue that the latter is emphatically the case.

Scolopendropsis duplicata is unambiguously a member of a clade that includes *Scolopendropsis* and *Rhoda* Meinert, 1886. This group is wholly endemic to Brazil apart from a record of “*Rhoda calcarata*” (= *Scolopendropsis bahiensis* fide Schileyko 2006) in Peru (Bücherl 1943). Several synapomorphies are strictly unique to *Scolopendropsis* and *Rhoda*, whereas others are observed in certain species of some of the large genera of Scolopendrini (*Scolopendra* Linnaeus, 1758 and/or *Cormocephalus* Newport, 1844), as follows:

- 1) a relatively small cephalic plate, much narrower than tergite 1 (T1);
- 2) a posterior median suture on the cephalic plate (Fig. 6). This feature is rarely observed in other scolopendrids (e.g., in *Cormocephalus mediosulcatus* Attems, 1928);
- 3) a strong longitudinal median suture on the coxosternum that splits into two divergent posterior sutures, crossed by a transverse suture at the division point (Figs. 2, 7);
- 4) intersclerite membrane being inconspicuous between the pleurites, which include a set of longitudinal pleural sclerites (cf. Schileyko 2006: fig. 4 for *S. bahiensis*) stacked atop each other on the dorsal part of the pleuron (Fig. 12). A similar morphology is rarely observed elsewhere in Scolopendridae, e.g., in *Cormocephalus mediosulcatus* (Attems 1930, fig. 114);
- 5) tarsi 1 of the locomotory legs half the length of tarsi 2 (Fig. 13);
- 6) pretarsi of the locomotory legs showing an abrupt transition from a pale-coloured proximal third to a strongly pigmented distal two-thirds (Fig. 14) that has a concave ventral surface bounded by sharp marginal ridges;
- 7) flattened dorsal and medial faces of the prefemora and femora of the ultimate legs;

- 8) dorsomedial and ventromedial rows of spines on the ultimate prefemur, each with 2–5 spines;
9) ultimate pretarsus strongly falcate, its ventral surface bearing a sharply serrated ridge [elsewhere seen in *Cormocephalus gervaisianus* (C.L. Koch, 1841) (Attems 1930, fig. 122)].



FIGURE 1. *Scolopendropsis duplicata* n. sp. Paratype MNRJ 15306. Lateral view. Scale bar, 1 mm.

Numerous additional characters are also plausibly synapomorphic for *Scolopendropsis* and *Rhoda* but because they are observed in several different groups of Scolopendromorpha they may be less reliable for taxonomic purposes. Such characters include the following: a marked distal taper of the antenna; elongation of the ultimate segment to about one and a half times the length of the penultimate; a complete median longitudinal suture on the ultimate tergite; margination confined to the ultimate tergite; the pore field on the coxopleuron separated from a similarly wide field devoid of pores by a sharply incised longitudinal sulcus (a similar sulcus is known within *Cormocephalus*, e.g., Lewis 2001, figs. 25, 29); and strongly thickened, forcipulate ultimate legs. The latter resemble those of some species of *Cormocephalus* (e.g., Attems 1930, fig. 121; Lewis 2001, figs. 12, 13) and the plutoniumines *Plutonium* Cavanna, 1881 and *Theatops* Newport, 1844.

Although the number of trunk segments in *S. duplicata* is within the range of Geophilomorpha, and indeed corresponds to a plausible ancestral number for that order as a whole, its phylogenetic status as deeply nested within the Scolopendromorpha is beyond question. The clade composed of *Scolopendropsis* and *Rhoda* possesses all of the apomorphic characters of the monophyletic family Scolopendridae, such as four ocelli in a rhomboid arrangement, sparsely hirsute basal antennal articles, and setae on the locomotory legs that are sparse and fine. It is likewise a member of more restricted clades within the Scolopendridae (see Edgecombe & Koch 2008 for cladistic analysis of Scolopendromorpha including *Scolopendropsis bahiensis*) as was recognised in previous classification within the subfamily Scolopendrinae and tribe Scolopendrini (e.g., Attems 1930). *Scolopendropsis* and *Rhoda* are members of the Scolopendrinae based on the synapomorphic orienta-

tion and structure of the spiracles, with their long axes oriented horizontally and a three-valved flap covering the subatrial cavity (Fig. 12), as well as complete paramedian sutures on the sternum along the length of the trunk (Fig. 14). The Brazilian clade is more deeply nested within the tribe Scolopendrini based on a shared distomedial prefemoral process on the ultimate leg.

The characters listed above provide clear evidence that *Scolopendropsis duplicata* and *S. bahiensis* derive from scolopendrid ancestors with 21 pairs of trunk legs, a fixed number in the family apart from the occurrence of 23-legged populations in the latter species and higher numbers in the former. It is unparsimonious to view the geophilomorph-like segment count of *S. duplicata* as evidence for a phylogenetic placement of this genus at the base of the Scolopendromorpha. That hypothesis would force reversals of the apomorphies of Scolopendridae, Scolopendrinae, and Scolopendrini listed above in an attempt to salvage a single character of segmentation. The elongate trunk of *S. duplicata* is convergent with that in geophilomorphs.

The congeneric relationship between *Scolopendropsis bahiensis* and *S. duplicata* demonstrates that destabilization of segment numbers, otherwise fixed in scolopendromorph species, is confined to a single clade. The diagnosis of Scolopendromorpha needs to be revised from 21 or 23 trunk segments to 21, 23, 39 or 43 segments.

Repository acronyms are as follows: BMNH—Natural History Museum, London, UK; IBSP—Instituto Butantan, São Paulo, Brazil; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MNRJ—Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MZSP—Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NCSM—North Carolina State Museum of Natural Sciences, Raleigh, North Carolina, USA; NMNH—National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA. Descriptive terminology follows Lewis *et al.* (2005).

Taxonomy

Order Scolopendromorpha Pocock, 1895

Diagnosis: Epimorpha with 21, 23, 39 or 43 leg-bearing trunk segments. Eye a cluster of four ocelli, single ocellus or absent. Antenna with 17–34 (usually 17–21) articles. Single tergite covers maxillipede and first leg-bearing trunk segments. Trunk heterotergy slight, distinct in at least anterior segments. Four laminae of mandible intersect at cruciform suture. Curled appendages along inner margin of telopodite of first maxilla. Tarsus of second maxilla with dorsal brush. Single row of bullet-shaped sensilla at border between labral and clypeal parts of epipharynx. Foregut relatively long, differentiated into crop and gizzard. Muscles attach to dorsal and ventral sides of spiracular pouches. Genital segments retracted above ultimate sternite. Gonopods lacking in female and usually in males, the latter with genital appendage on first genital segment in some species of a few genera. Left ejaculatory duct rudimentary or absent. Spermatophore bean-shaped, with multilayered wall.

Remarks: In light of the discovery of previously unknown variability in trunk segmentation in Scolopendromorpha, the order is rediagnosed with emphasis on strictly autapomorphic characters.

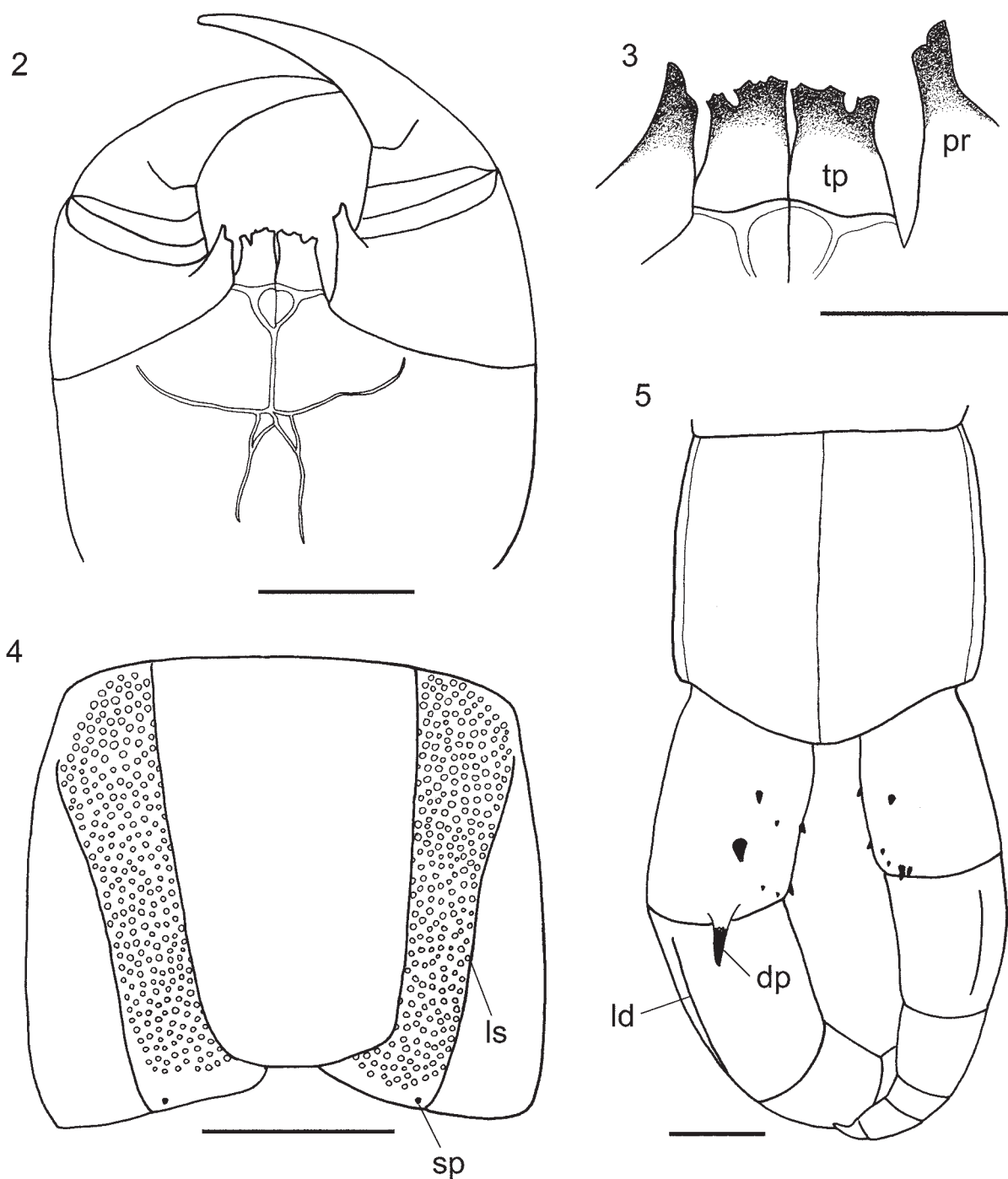
Family Scolopendridae Leach, 1815

Subfamily Scolopendrinae Leach, 1815

Tribe Scolopendrini Leach, 1815

Genus *Scolopendropsis* Brandt, 1841

Type species: *Scolopendra bahiensis* (Brandt, 1841), by monotypy.



FIGURES 2–5. *Scolopendropsis duplicata* n. sp. Holotype MNRJ 15258. 2, forcipulae; 3, tooth plates (tp) and processes of trochanteroprefemora (pr) of forcipulae; 4, sternite and coxopleurae of segment 43; 5, segment 43 and ultimate legs, dorsal view. Scale bars, 0.5 mm. Additional abbreviations: dp, distomedial prefemoral process; ld, longitudinal depression on femur; ls, longitudinal sulcus delimiting pore field; sp, spine at posterior border of coxopleuron.

***Scolopendropsis duplicata* n. sp.**

Figs. 1–14.

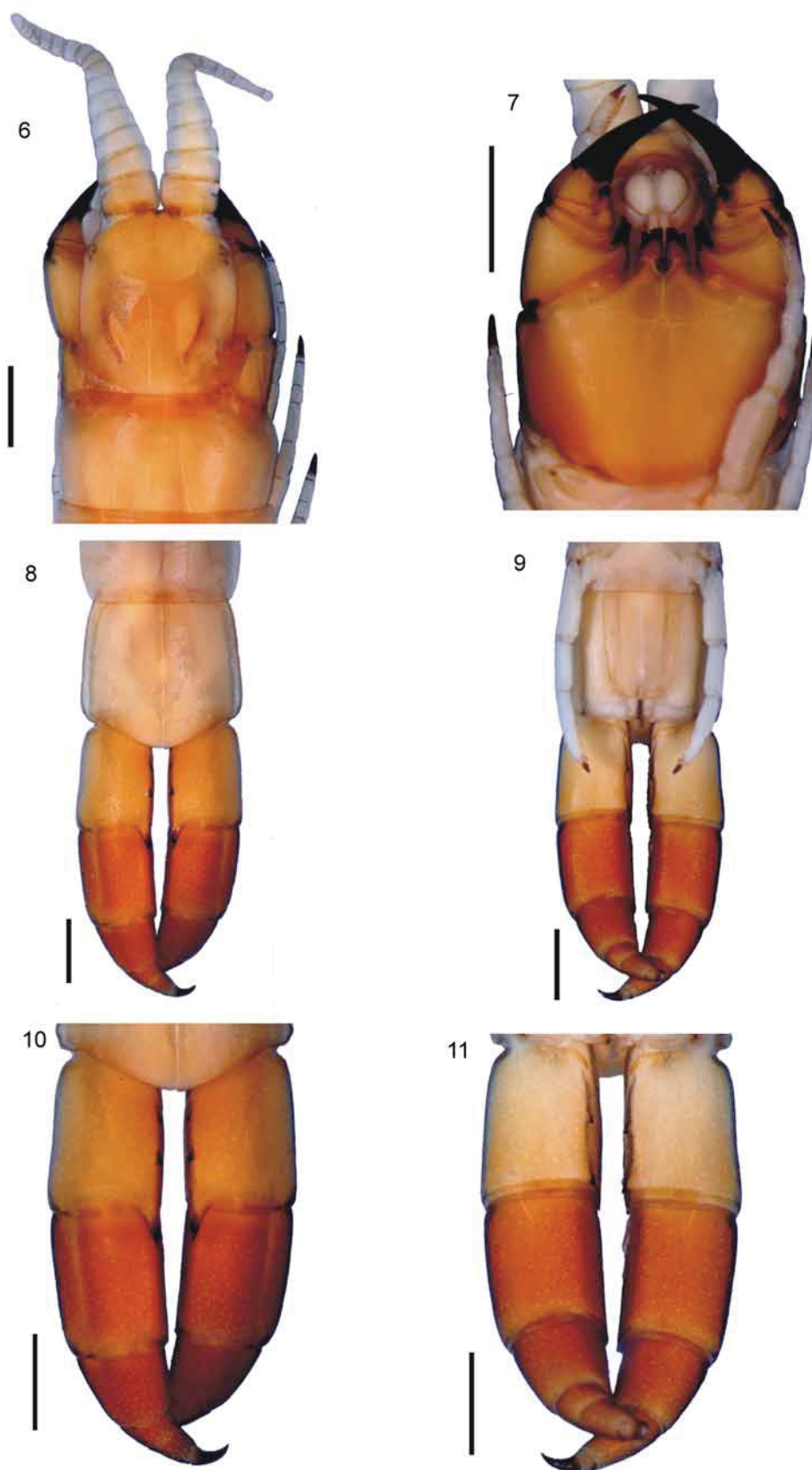
Diagnosis: Thirty-nine or 43 trunk segments; paramedian sutures of T1 incomplete anteriorly, extending $\frac{3}{4}$ of length; posterior border of coxopleuron usually bearing single short spine caudal to posterolateral corner of

pore field; ultimate leg prefemur with two ventromedial and one to three dorsomedial spines in longitudinal rows (when multiple), the dorsomedial row aligned with prefemoral process; latter with two or three apical spines; flattened medial face of prefemur variably bearing one to six small spines that, when maximally developed, are aligned in two rows; posterior halves of ultimate leg prefemur and femur with sulcus-like longitudinal depression dorsad.

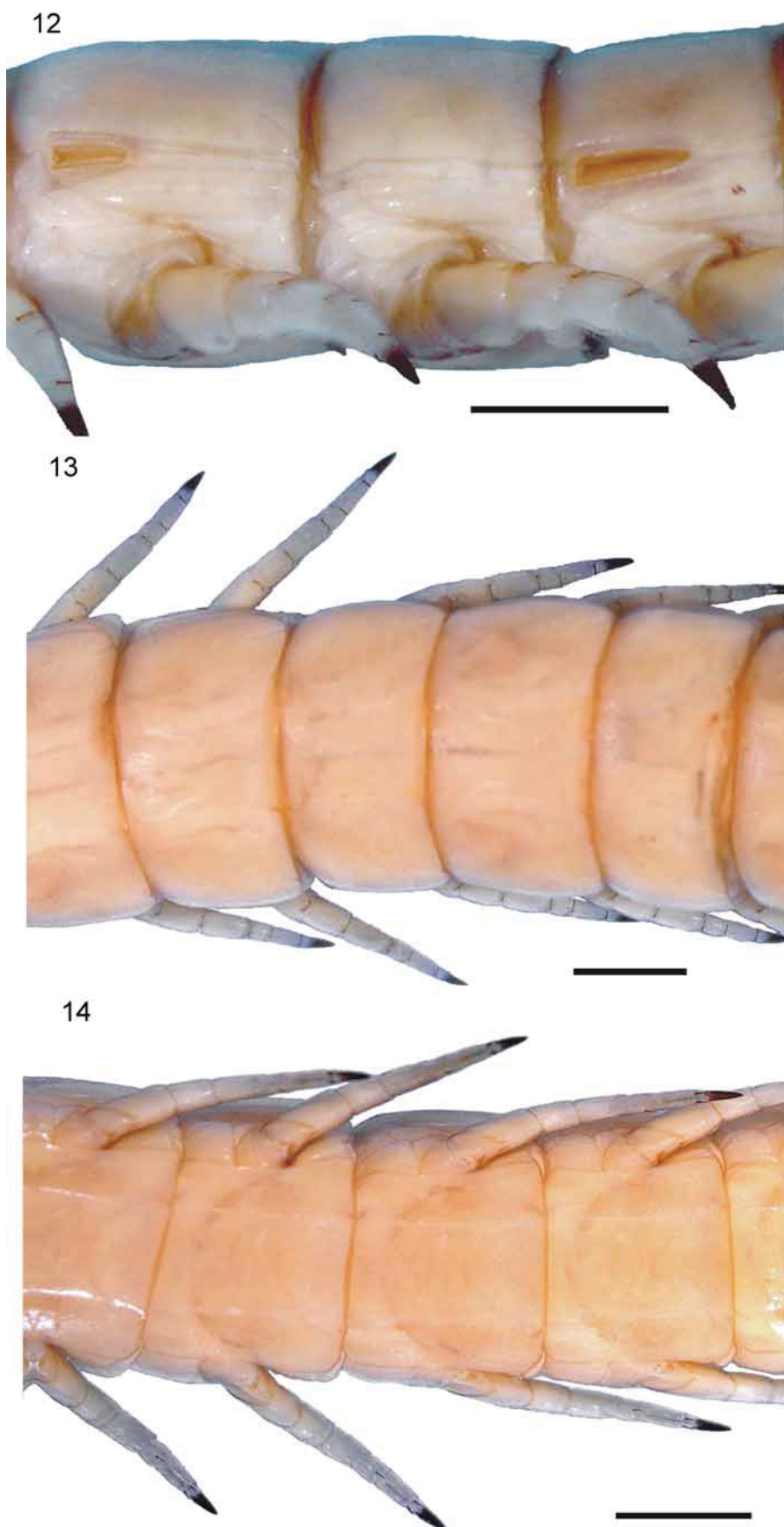
Type specimens: Segment number (39 or 43) indicated in parentheses. Holotype MNRJ 15258, 1 ex., Tocantins State, Porto Nacional, 10.0589°S 48.412°W, 22L 0783671 UTM 8886955, 29.IX–07.X.2001, D. Pavan (43). Paratypes all from type locality, leg. D. Pavan unless indicated otherwise: paratype MNRJ 15259, 1 ex., 29.IX–07.X.2001 (39); MNRJ 15305, 1 ex., 29.X–07.X.2001 (43); MNRJ 15306, 6 ex., 29.IX–07.X.2001 (39); IBSP 1519, 1 ex., Ribeirão Santa Luzia, Fazenda Sandoval, 2000, Equipe Investco/Ulbra (43); IBSP 1498, 1 ex., 07–11.VIII.2000, I. Knysak, R. Martins & G. Puerto (43); IBSP 2406, 1 ex., Ribeirão Santa Luzia, Fazenda Sandoval, 10–13.VII.2000, Equipe Investco/Ulbra (39); IBSP 2843, 1 ex., Fazenda Sandoval, 11.VIII.2000, I. Knysak, R. Martins & G. Puerto (43); IBSP 2392, 2 ex., Fazenda Sandoval, 5–10.V.2000, I. Knysak, R. Martins & G. Puerto (43); NMNH, 1 ex., 29.IX–07.X.2001 (39); MCZ, 1 ex., 29.IX–07.X.2001 (39); NCSM, 2 ex., 29.IX–07.X.2001 (43, 39); MZSP, 3 ex., 29.IX–07.X.2001 (43, 39); BMNH, 2 ex., 29.IX–07.X.2001 (39).

Etymology: The specific name refers to the near doubling of trunk segment numbers compared to the most closely related species.

Description: Length of 39-segmented individuals ranging from 31–74 mm; that of 43-segmented individuals from 53–78 mm. Cephalic plate, trunk and legs yellow in specimens preserved in alcohol; forcipulae and ultimate legs orange. *Cephalic plate:* smooth, 1.3 times as long as wide, distinctly narrower than T1, with four ocelli on each side. Posterior longitudinal median suture extending for $\frac{1}{2}$ – $\frac{3}{4}$ of length (Fig. 6), difficult to detect in juveniles. Posterior border overlain by T1; basal plates at posterolateral corners delimited by continuous suture across posteromedial margin. *Antennae:* short, usually reaching backwards to midlength of T1; with 17 articles, basal six glabrous/sparsely hirsute. *Coxosternum:* tooth plates about 1.3 times as long as wide (Figs. 3, 7); inner teeth fused, with two ill-defined cusps, lateral teeth isolated, apices slightly caudad to inner teeth; basal sutures approximately transverse. Longitudinal median suture bifurcating posteriorly into inverted Y-shape, crossed at or near division point by a subtransverse suture curving anteriad laterally and extending to forcipular bases (Figs. 2, 7). Process of forcipular trochanteroprefemur with two blunt apical denticles. *Second maxilla:* symmetrical accessory claws on each side of apical claw. Coxosternum with complete median sulcus. *Tergites:* smooth; T1 with paramedian sutures on posterior $\frac{3}{4}$ (Fig. 6); TT2–38 or TT2–42 with complete paramedian sutures; ultimate tergite (T39 or T43) about 1.5 times as long as penultimate, with complete median longitudinal suture (Figs. 5, 8). Margination on ultimate tergite only. Pretergites usually present on the posterior segments. *Sternites:* smooth; complete paramedian sutures present on SS2–38 or SS2–42 (Fig. 14). Ultimate sternite considerably longer than wide (Figs. 4, 9), lateral margins gently converging caudad, with median longitudinal depression; posterior margin gently convex or straight. *Spiracles:* on segments 3, 5, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30, 32, 34, 36, 38 of all specimens; those with 43 trunk segments additionally bear spiracles on segments 40 and 42. Anteriormost spiracle enlarged relative to others, nearly half length of T3; second spiracle (segment 5) only slightly larger than those immediately more posterior. Longitudinal pleurites parallel to trunk axis (Fig. 12). *Coxopleura:* longer than wide, pore field half as wide as coxopleuron, separated from pore-free part of pleuron by well-incised longitudinal sulcus; posterior border of coxopleuron bearing short spine immediately caudal to posterolateral corner of pore field (Fig. 4), usually present on only one side, sometimes absent in specimens with 39 leg-bearing segments. Posterior border of coxopleuron abruptly truncated, coxopleural process absent. *Legs:* tarsi composed of two articles. Tarsus 1 shorter than tarsus 2. Spur present on tarsus 1 of legs 1–37 or 1–41; ultimate and penultimate legs lacking spur. Pretarsus longer or equal in length to tarsus 2; proximal $\frac{1}{3}$ pale, distal $\frac{2}{3}$ strongly pigmented with concave ventral surface bounded on each side by sharp marginal ridge; pretarsi of legs 1–38 or 1–42 with two accessory spurs



FIGURES 6–11. *Scolopendropsis duplicata* n. sp. Paratype MNRJ 2392. 6, cephalic plate and T1; 7, forcipular coxosternum; 8, segment 43 and ultimate legs, dorsal view; 9, segment 43 and ultimate legs, ventral view; 10, ultimate legs, dorsal view; 11, ultimate legs, ventral view. Scale bars, 1 mm.



FIGURES 12–14. *Scolopendropsis duplicata* n. sp. Paratype MNRJ 2392. 12, trunk segments 3–5, lateral view; 13, trunk segments 7–12, dorsal view; 14, trunk segments 7–11, ventral view. Scale bars, 1 mm.

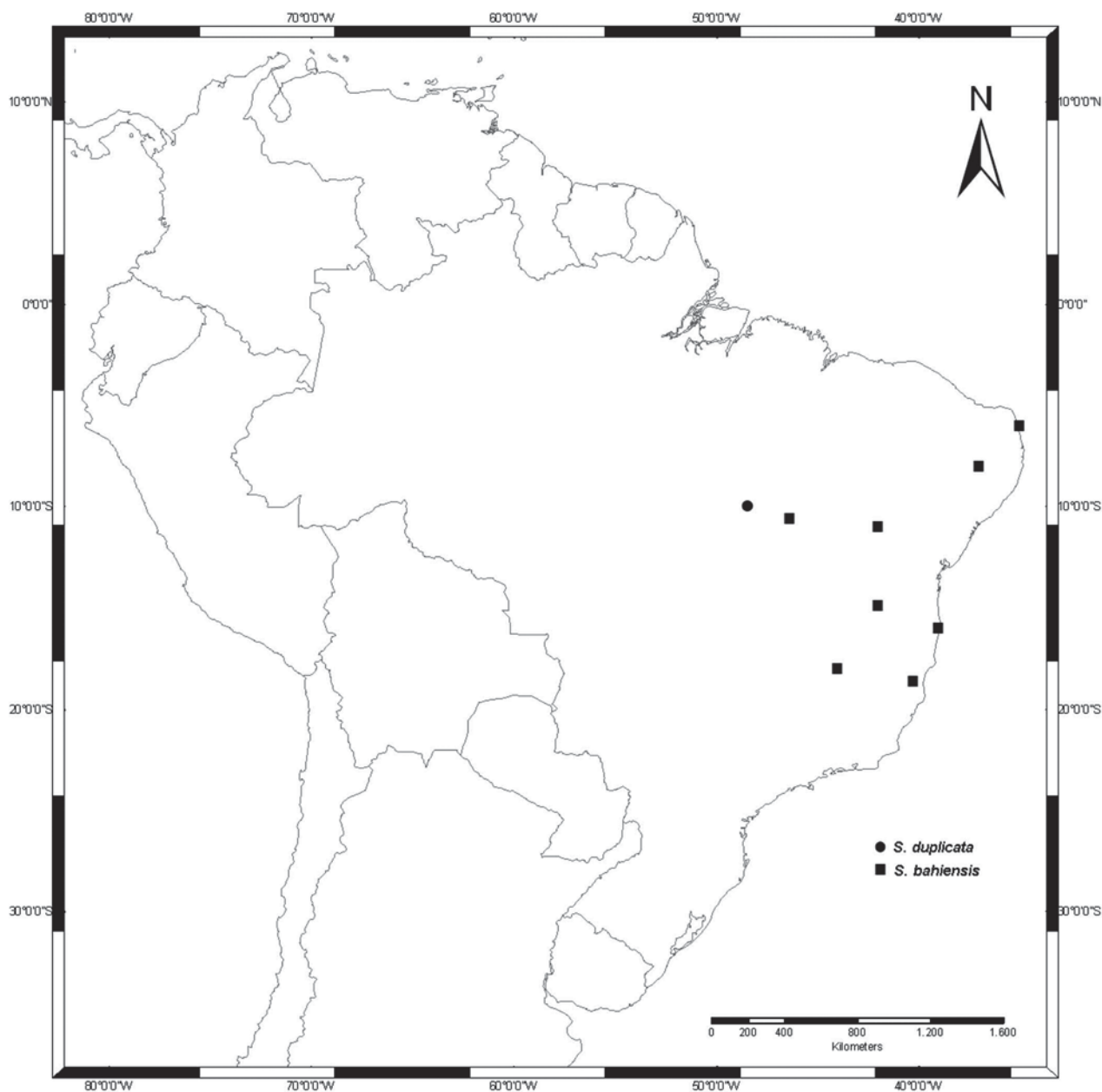


FIGURE 15. South America, with dot indicating type locality of *Scolopendropsis duplicata* n. sp. (Brazil: Tocantins State: Porto Nacional). The distribution of *S. bahiensis* (Brandt, 1841) is indicated by black squares.

about $\frac{1}{4}$ as long as pretarsi on anterior segments, increasing to about $\frac{1}{3}$ length of pretarsi on posterior segments. *Ultimate legs*: thickened, forcipulate, with relatively short articles; prefemora with two ventromedial and one to three dorsomedial spines in longitudinal rows (when multiple), the dorsomedial row aligned with distomedial process (Figs. 5, 10); the latter conical, bearing two or three small apical spines. Medial face of prefemur flattened, variably bearing one to six small spines that, when maximally developed, are aligned in two rows. Posterior halves of prefemur and femur with sulci-like longitudinal depressions on dorsal side (Fig. 10). Pretarsus with one basal accessory spur, shorter than those on ambulatory legs; ventral surface of pretarsus with serrated ridge bearing numerous small, sharp teeth.

Distribution: Brazil, Tocantins State. *Scolopendropsis duplicata* is restricted to typical “cerrado” vegetation, and is known only from its type locality (Fig. 15).

Discussion: Despite the fact that this new species differs from all other Scolopendromorpha with respect to a character (trunk segment number) that is routinely used to diagnose genera or families within the order, the highly detailed similarity to *Scolopendropsis bahiensis* in all morphological characters apart from trunk segmentation leads us to favour its congeneric classification. We note the paradox that variability in scolopendromorph segmentation is a remarkable discovery, and yet *S. duplicata* and *S. bahiensis* are so similar in other respects and their sister group relationship so highly corroborated that generic separation is unwarranted. The discovery of segmental polymorphism in *S. duplicata* suggests that Schileyko (2006) was correct in interpreting *S. bahiensis* as also polymorphic. More evidence is now available demonstrating that segmental polymorphism is indeed possible in a scolopendromorph species and more specifically is known within this restricted clade.

Because the genitalia are concealed beneath the genital sternite, we have not amassed an adequate sample size to determine how segmental polymorphism correlates with sex. Dissected individuals with 39 segments include ones with spermatophores, confirming that at least some are males. Spermatophores are lacking in dissected 43-segmented specimens, but we have not ascertained whether they are invariably females. Even if some exceptions are eventually found to the possible rule that males in this species have 39 segments and females have 43, *S. duplicata* is likely to represent the first example of sexual dimorphism in segment number in non-geophilomorph centipedes.

Most specimens of *S. duplicata* were found in pitfall traps for reptiles and amphibians in the dry, xeric “cerrado”, a vegetation typical of central Brazil. All specimens were collected before flooding of the Luis Eduardo Magalhães hydroelectric power plant, in the Tocantins River, and the type locality is now under water. Vegetation around the lake is the same as that at the now submerged type locality. An expedition organized by the first author in June 2007 failed to discover any specimens of *S. duplicata*, even though a forest patch 500 m away from the type locality was sampled. Thus, the original habitat of this species may have been impacted by the flooding of the hydroelectric power plant, and further expeditions are needed to seek additional individuals of this remarkable Brazilian species. Also noteworthy is the fact that a closely related species, *Rhoda spinifer* (Kraepelin, 1903), occurs sympatrically on the left bank of the Tocantins River.

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